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THE BEARING OF SOME GENERAL BIOLOGICAL FACTS ON BUD-VARIATION[1]

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I take it no one denies that in the Angiosperms variations may be produced in connection with reproduction by means of buds and that these variations may be perpetuated by the same method. Practically, as horticulturists and plant breeders, we care little about the occurrence of bud-variations elsewhere in the organic world. Nevertheless, it may help in the orientation of our ideas if we remember that budding is not a rare or unconventional method of reproduction. In a generalized form, the earliest method, it has persisted throughout the plant kingdom from the most primitive to the highest and most specialized types. Sexual reproduction has not replaced it, but has been added to it. Even in the animal kingdom, though eliminated among the higher forms, it still exists as an occasional alternate method in three fourths of the phyla. Such being the case, it would seem logically to follow that variation must have been within its possibilities.

The cause, the frequency, the type, the constancy, the mechanism, of these variations are more debatable, however, and on these questions many biological facts which superficially seem unconnected, have a direct bearing. In

[1] Read before the meeting of the Society for Horticultural Science, December 28, 1916.

fact, on certain phases circumstantial evidence is the only evidence at hand.

The exact nature of the cause or causes of bud-variation can hardly be discussed profitably. We may imagine irregularities of cell division directed by combinations of unknown factors, but to describe these factors in concrete terms is at present impossible. At the same time, cause can not be neglected entirely even at present, for cause in a generalized sense is intimately connected with frequency in that vigorous perennial the question of the inheritance of acquired characters. The data on this subject are so voluminous that each for himself must give them careful conscientious consideration. Here no more can be done than to point out some of the conclusions to which I, personally, have been driven, and their connection with the subject in hand. These conclusions are:

1. Broad and varied circumstantial evidence indicates unmistakably that the inheritance of acquired characters has played an extremely important rôle in evolution.

2. Numerous experimental investigations designed to test the possibility of such inheritance directly have either failed utterly or have been open to serious destructive criticism. Direct proof of the inheritance of acquired characters is therefore lacking.

3. If conclusions 1 and 2 are to be harmonized, either modifications are fully inherited so rarely that proof that they do not belong to the general category of chance changes in constitution of the germ-plasm is impossible, or the imprint of the environment is so weak that extremely long periods of time—perhaps geological epochs—are necessary for its manifestation.

Diametrically opposed views on the inheritance of acquired characters are held tenaciously and unequivocally by equally eminent biologists. Those who concur with the Lamarckian position are nearly always the students of evolution who approach the subject from the historical or the philosophical side and who rely almost entirely on circumstantial evidence; those who adhere to the side

of Weismann are usually experimentalists whose evidence is indeed direct, but often questionable, usually capable of various interpretations, and always fragmentary. I have been bold enough to grasp both horns of the dilemma, and to plead that each is right from his point of view. My confession of faith is, the environment has been an immense factor in organic evolution, but its effects are shown either so infrequently or after the elapse of so great a time, that for the practical purposes of plant breeding we can neglect it as we would neglect an infinitesimal in a calculation. As Bergson, I think, said:

> We have been trying to prove that the hour hand moves, in a second of time.

A few words will make clear the general arguments in favor of this position, although adequate support to the thesis would require considerable time.

In the first place, it seems to me the possibility of the inheritance of acquirements must be admitted. Weismann's general contention that the chromatin of the germ-cells is the actual hereditary substance, and that the germ-cells themselves may be regarded as one-celled organisms reproducing by fission and conjugating at certain times, while the body must be considered simply an appendage thrown off from and independent of the germ-cells, is not supported merely by the embryological researches of Boveri, Kahle and Hegner on two or three animal forms, or by the ingenious ovarian transplantations made by Castle and Phillips on guinea pigs, but by all of the recent pedigree culture and cytological genetic work, botanical as well as zoological. Nevertheless it has not been and logically can not be proven that there is no way for environmental forces to produce germ-plasmic changes. Memory is just as strange a phenomenon and Semon has done biology a service by pointing out the analogy between the mechanical requirements for memory and for the inheritance of somatic modifications.

This possibility being admitted, one may well concede the plausibility of the arguments of the numerous pale-

ontologists, taxonomists and ecologists in favor of Lamarckian principles, in spite of the fact that their evidence is circumstantial. They take a comprehensive view of the actual conditions that exist among organisms, which is impossible to the experimentalist. It will not do simply to say that the manifest convergence of analogous organs in all parts of the organic world, or the wonderful adaptations of the social insects *may be explained in some other way.* Of course there may be other explanations for these phenomena; but until more satisfactory explanations are forthcoming it is rightfully a custom in science that the adequate interpretation at hand should be accepted.

On the other hand it is equally wrong for the ardent devotees of Lamarckism to clutch at every isolated case, every inadequate and abortive experiment, when judicial consideration shows not a single *unassailable* instance of the inheritance of a somatic modification. Many of these experiments have a direct bearing on bud-variation, and I shall attempt to show where they lead us.

1. *Inheritance of Mutilations.*—The most radical Lamarckians of the present day only go so far as to suppose that mutilations are inherited on very rare occasions—and they are always zoologists. Ethnology has furnished us with so many histories of mutilations of ears, of lips, of feet, of reproductive organs, long continued in the folkways of a people, that new laboratory experiments have been deserving of the ridicule they have received. Botanists have seldom had any delusions on the subject. Plants are so continually mutilated in the buffetings they receive during life, with no result in the next generation, that the non-inheritance of the effects of such injuries is taken as a matter of course. Yet there is occasionally one whose reason fails at the critical moment, and who holds that cuttings from the chrysanthemum with the large flower resulting from the removal of lateral branches, will produce larger flowers in the next generation than will an untreated sister plant. If not this, some equally indefensible doctrine.

2. *Effects of Changed Food Supply.*—This last example was really one of changed food supply induced by mutilation. Change of food supply by other methods has been the basis of scores of experiments, particularly on insects. Many insects are so very whimsical about what they eat that it seems possible their selective appetite may be an inherited instinct impressed by the environment of countless generations. But the total result of all experiments on them is merely to prove that a second generation may be influenced in the start they get in life by the nutrition of the mother.

The same thing is true in plants. We fertilize a pop corn to get a bumper crop of good plump healthy seeds, but we don't expect a dent corn as the next year's result. We very properly endeavor to give our potatoes a balanced ration, in expectancy of a larger yield of well-matured, healthy tubers, but we should not expect these tubers to affect our next season's supply other than by their health. Similarly we take scions from well-lighted parts of the tree where growth has been good. In such twigs the graft union heals easily and properly, and a fit channel for conveying nutrients is established. In doing these things we are practising sanitation or preventive medicine, as it were, a laudable proceeding. But the horticulturist who promises a *different variety* by such means is illogical and misleading.

Yet we find Bailey so imbued with the idea of making out a perfect case for Lamarckism that he lends the weight of his authority to the following statement among others:[2]

> Whilst these "sports" are well known to horticulturists they are generally considered to be rare, but nothing can be farther from the truth. As a matter of fact, every branch of a tree is different from every other branch, and when the difference is sufficient to attract attention, or to have commercial value, it is propagated and called a "sport."

We may admit the differences between the branches of a tree without cavil. What is more serious is the impli-

[2] "Survival of the Unlike," p. 72.

cation to the reader that all variations have the same coefficients of heredity, that a bud-variation is simply a wide fluctuation imposed by external conditions. If this were true the whole organic world would be chaos. But species and varieties do exist. They may be "judgments" in one sense, but in another they are concrete things. In fact we learn this further on in this volume when it suits Bailey's purpose to have asexually propagated varieties very constant. He says (p. 353):

> At first thought this fact—that varieties may be self-sterile—looks strange, but it is after all what we should expect, because any variety of tree fruits, being propagated by buds, is really but a multiplication of one original plant, and all the trees which spring from this original are expected to reproduce its characters.

3. *The Effects of Disease.*—The influence of disease is in many ways like that of malnutrition, in that it is wholly an effect on the physiological efficiency of the reproducing cells. This fact is fairly clear when dealing with diseases with outstanding symptoms. In many instances, however, diseases are not easily diagnosed. There may even be no suspicion that disease is present. In such cases it is rather hard to believe that selection is not accomplishing a positive and radical improvement. A good example of this is the selection of potato tubers. No one consciously selects a seed potato infected with blight. Independent of the probability of reinfection, there is the likelihood that the diseased tuber will not be able to produce a normal plant because of the effect the fungus has had on its own cells. One doesn't usually believe, however, that rejection of this tuber and selection of the healthy sister is going to lead to the formation of a new race. Yet numerous experiments on potatoes in which it is shown that successive selections have raised the average yield over that of the unselected tubers, are probably of just this type. The race is kept up by the rejection of diseased tubers, but there is no evidence whatever that it is *improved*. I am not going to argue that desirable asexual variations may not occur during this time, and be retained. I say only that any improvement

indicated by the raw data, must be discounted by the amount of deterioration shown by the unselected variety under similar conditions. Such deterioration is very common, and is due to disease, I believe, rather than to any supposed disadvantage of asexual reproduction *per se.*

This category of facts has been cited under the discussion of the inheritance of acquired characters, because such phenomena have perplexed other than botanists. Belief in the transmission of disease, or the effects of disease, by sexual reproduction was current for many years. It is only since the possibility of infection in the egg itself was demonstrated for various diseases, that the true state of affairs has been known.

Many other types of experiments designed to demonstrate Lamarckism might be cited, but they have no direct bearing on bud-variation except in so far as a positive case would affect our general attitude on the frequency of their occurrence. They are all similarly negative or questionable, however, so that we must conclude with Weismann that no case of inheritance of acquirements has been proved beyond a reasonable doubt. In other words we grant such a possibility but believe it to be so rare or so gradual that practically it may be disregarded.

In reality one could hardly have expected any other conclusion from the type of experiment by which the question has been attacked. Generalized they are something like this. Species X having been grown under environment A for numerous generations is removed to environment B. An adaptive change occurs which persists during several generations. Later the descendants of the original plants are returned to environment A and the change is reversed. When the reverse change occurs more slowly than the original change, it is argued that Lamarckian inheritance is shown. The logic used to draw such a conclusion is indefensible, even if the difficulty of correcting properly for changes due to normal heredity is left out of consideration.

If acquired characters are inherited and the changes

induced are reversible, the long period under environment A should have produced a deep impression on species X. Change under environment B should be slow. Reversal should be rapid, however, because of the slight impression environment B must be supposed to have made during the very few generations in which its influence was possible.

If acquired characters *are not inherited,* precisely the same changes should occur, owing to somatic adaptation, the only differences being that the total amount of change in each case would be reached in the second generation after the environment had acted during the earliest stages of the life history.

If, on the other hand, the changes induced by environment B are not reversible, judgment must be based on the percentage of individuals changed by B and not rechanged by A. One can readily see how a just judgment would be clouded by probable reversible somatic effects in such cases. Instances of the inheritance of acquirements, unless they were very frequent, which from our general evidence is unthinkable, would be indistinguishable from ordinary chance variations.

Such methods of attack on the subject being almost predestined to failure from the inherent difficulties of the problem, it would seem wiser to seek for a more hopeful methodology, and in the meantime to accept the only conclusion justified by the data at hand; namely, the inheritance of acquired characters is either so rare an occurrence or so slow a process, that by plant-breeders it may be assumed to be non-existent. One realizes of course that the problem of sexual transmission of somatic acquirements is not necessarily the same as that of asexual transmission, but the experimental results have been the same in both cases. Let us, admit, therefore, that one can not hope to obtain real improvement in asexually propagated varieties merely by selecting buds from plants or parts of plants which have developed under especially favorable conditions.

This does not mean that radical environmental changes

may not be the direct cause of such a modification. Dr. H. J. Webber once informed the writer that immediately after the great Florida freeze of the early nineties bud-variations in the citrus fruits of that region were greatly increased. Such variations may have been induced by the freezing, but they were not adaptive variations.

The conclusions reached thus far have not involved a point of theory which practically is difficult to separate from the one just discussed. It is this. If we disregard adaptive variations, is there not still a reason for selecting fluctuations? Are there not internal factors which so act that there is a narrow but appreciable variability in an asexually produced population which may offer a basis for selection? In other words, how constant is an asexually propagated race?

We can make an effort to compute the frequency of marked bud-variations. But have we any right to assume that these represent the sum total of all bud-variations? Are not bud-variations and perhaps all inherited variations like residual errors, the small ones frequent, the large ones rare? This may be the case, but I should like to emphasize the fact that we have no true criterion for determining the size of a variation. A variation that appears large by visual criteria may be an extremely small change in the constitution of the plant, and *vice versa*. In view of this fact together with the practical consideration that commercially valuable variations must be measurable within a reasonable duration of time—say a lifetime—it is by no means certain that we are going far astray in calculating the frequency of bud-variations by the so-called marked jumps or mutations.

Furthermore the range of the fluctuations of asexually propagated varieties of most species is very small even when broadened—as it always is—by the addition of the effects of variable external conditions. It is not hard to recognize a Winesap apple, a Clapp's Favorite pear or a Concord grape, even though these varieties have been grown extensively for a considerable number of years. Certain local subvarieties of the pome fruits are said to

exist, but they are so extremely rare that one may admit all cases of disputed origin and still have very little asexual variation to account for.

I have never seen a published calculation of the frequency of bud-variation, and presume it would be of little value anyway, since the general evidence indicates a different frequency for different species and even for the same species at different times. It may be mentioned, however, that in personal examination of over 100,000 hills of potatoes belonging to several hundred varieties, 12 definite bud-variations have been seen, a frequency of 1 in 10,000; while just as careful a scrutiny of about 200,000 plants belonging to the genus *Nicotiana* has brought to light but 1 case.

Probably a more practical and just as satisfactory an estimate of the frequency of bud-variations in economic plants is the record of varieties that have been produced in this manner. Naturally such a record contributes little to theory because only a portion of the variations arising are observed, and only a fraction of those observed are propagated. Further, the origin of comparatively few commercial varieties is known. Yet we may get some idea of what to expect in the future, by noting what has occurred in the past.

Data gathered in this manner will appear to give us different values depending on how we approach the matter. For example, in Cramer's wonderful monograph on bud-variation, the grape is cited as one of the species that often varies in this manner. He cites some 25 or more such varieties. Yet in the large list of American grapes in Hedrick's "Grapes of New York" only one doubtful case of bud-origin is reported. When one remembers that hundreds of varieties of grapes are grown and millions of vines are examined each year, improvement by this method seems rather hopeless. And examination of the list of present-day apples, pears, plums and cherries, of the bush-fruits, or of potatoes—all groups of considerable horticultural importance—is still more disappointing, for I venture to say that the varieties of

these types in cultivation which have originated as bud-variations can be counted on the fingers of one hand.

At the same time it would be wrong not to attribute any importance to bud-variation as a plant breeding adjunct. Cramer lists several hundred chrysanthemums and over a hundred roses as of bud-origin, as well as a smaller number of varieties in species where bud-variation appears to be less prevalent. Further, Shamel is said to have found bud-variation in the citrus-fruits to be sufficiently common to be worthy of an extended investigation.

These species, however, with perhaps the banana and the pineapple—the origin of whose varieties is little known—are the outstanding examples of comparatively frequent bud-variation, picked from our whole long list of cultivated plants. The first two examples, moreover, are species belonging to the domain of floriculture, where rather superficial characters such as color are valuable. In very few other species have bud-variations been recorded in sufficient numbers to justify us in employing any other adjective than "rare" in describing them. And of the sum total of these varieties only an extremely small percentage are of such a nature that agriculture would suffer a material loss if they were eliminated.

Perhaps these last statements appear to imply a very limited type of bud-variations. This is not true. Bud-variations are wholly comparable to seed-variations in their nature, but they are handicapped because recombinations of variant characters are possible only in sexual reproduction. N bud-variations in a species are simply N variations, but N seed-variations may become 2^n seed-variations provided they are not linked together in heredity. An immense advantage thus accrues in favor of seminal reproduction because by far the greater number of commercially valuable characters are complex in their heredity, *i. e.,* they are represented in the germ-plasm by several factors independently inherited.

Cramer divides bud-variations into the same classes that de Vries has used for sexual mutations: progressive,

where new characters arise; retrogressive, where a character becomes latent or lost; and degressive, where latent characters become active. In this important monograph practically all recorded bud-variations to the date of publication, 1907, are discussed. Yet not a single case of *progressive* variation is listed. They are all catalogued as retrogressive or degressive. Their classification is correct, however, only when a progressive variation is defined as the addition of a character wholly unknown in the previous history of the species.

As examples of what bud-variation does produce we may well study Cramer's painstaking work. There are losses of thorns, hairs and other epidermal characters, together with an occasional degressive change of the same kind. There are changes in color in vegetative parts. Green becomes red or "aurea" yellow, or a loss of anthocyan occurs. Sometimes the changes are such that the plants remain striped or otherwise variegated. Flowers and fruits exhibit the same types of color variations in considerable numbers. They are mostly losses, with the appearance of what in Mendelian terminology is called hypostatic colors, but once in a great while epistatic colors recur anew.

Monstrosities appear. Other parts of the flower take on the appearance and form of petals or of sepals. Doubling occurs in several different ways. Fasciations arise. Changes in the character of the reproductive apparatus are not uncommon, sometimes giving us seedless fruits.

Plants change their habit of growth. They become dwarf. They retain juvenile characters. They become laciniate, or develop the trait known as "weeping."

Thus we see that bud-variation is not limited in its manifestations; and what is more important, we realize that bud-variations are very comparable to seminal variations, there being hardly a type of change known in sexually reproduced plants that has not been duplicated asexually. What then is the difference, if any, between true somatic changes and true germinal changes in constitution? We can get clues which indicate a fairly satis-

factory solution of this problem from three different lines of research, pedigree cultures, graft-hybrids and cell-studies.

It is a noteworthy fact that the character of the progeny produced sexually by bud-variations has been studied in a comparatively few cases, and in most of these instances self-pollinations were not made. Nevertheless Cramer believes the following conclusions are justified:

1. In a vegetative Mendelization, of the progeny of a branch with the positive character 75 per cent. have the character and 25 per cent. are without it, while the progeny of a branch without the character all lack it.

2. In a vegetative "Zwischenrasse" by which he generally means a variegated race, of the progeny of each type (original and variant), a part retain and a part lack the character, the percentage being variable.

3. In a vegetative mutation, by which he means any change not a "Zwischenrasse" and which did not appear to him to be Mendelian in type, of the progeny of a branch retaining the positive character, either all possessed it or a part were with and a part without it, while the progeny of a branch without the character were all of the same type.

If we allow for some deviation due to cross-pollination, I believe that Cramer's records support this view, and that modern genetic research suggests the interpretation.

In the first place, the "Zwischenrasse" are evidently of the type studied principally by Correns and by Baur in sexually reproducing races. They are due to chromatophore changes, and in many cases at least are not the result of nuclear activity. This being true, one would expect in neither asexual nor sexual reproduction the same type of inheritance for variegated races that obtains for other types of variation. Inheritance will parallel cytoplasmic rather than nuclear distribution; an expectation apparently realized for both types of reproduction.

Omitting the "Zwischenrassen" therefore, we have two phenomena to explain, both of which are similar to cases of inheritance in sexual reproduction where chromatin

distribution parallels the facts. In each instance the negative variant—may we call it the recessive—breeds true. In one case the positive variant breeds true, in the other case it gives a simple Mendelian ratio.

The mechanism necessary for such phenomena is not difficult to picture. Bud-variations are many times more frequent in hybrids, that is, in plants heterozygous for one or more characters, than they are in *pure* species. This is the view of Cramer, this was the view of Masters, the eminent English student of bud-variations and teratological phenomena, this was the conclusion drawn by the present writer in several articles published some years ago. Such results would be obtained either when the proper germinal change occurs in the chromosome whose mate lacks a character for which the plant is heterozygous; or, when there is a dichotomy in which the chromosomes of such a pair are not halved but pass the material basis necessary for the production of the positive character to one daughter cell and not to the other, provided the daughter cell lacking the character gives rise to a branch.

A bud-variation in a character for which the plant was homozygous would be obtained only when simultaneous like changes occur in both chromosomes of a homologous pair, or when the material basis necessary for the production of the positive character all passes to one daughter cell, as described above.

This hypothesis would account for the fact that heterozygotes give rise to bud-variations more frequently than homozygotes, since a germinal change seldom gives rise to a new positive character, and a change in one chromosome of an identical pair tending toward the production of a recessive, would not show in the latter case.

I am not certain that this hypothesis may not with reason be applied to variations that are usually considered seminal. There is no particular ground for assuming that such variations occur only at the maturation of the germ-cells. We know that progressive variations of whatever origin are extremely rare. Why then may not

most variations be produced in cell divisions previous to the formation of the germ-cells? When recessive we should not note them as bud-variations unless the plant is heterozygous and the mutating cell gives rise to a branch; when dominant we should only note them in the latter eventuality. But if these mutating cells should later give rise to germ-cells, the change would become apparent in the progeny.

We have still one other hypothetical case to consider. It is said that some bud-variations are not transmitted by seed. I have not been able to trace an authentic case, but such is the general belief, fathered, I think, by Darwin. The usual citation is the nectarine, which sometimes is said to give nectarines but at other times gives only peaches. Whether trichome characters only behave thus I do not know. But if that be true, we can understand why if we refer to Winkler's work on the so-called graft-hybrids.

Winkler found that the most interesting of these peculiar phenomena are caused by the tissue of one species growing around the tissue of the other. He therefore gave them the euphonious name of periclinal chimeras. Cytological examination showed that the epidermal tissues only are from one race, the remaining tissues being from the other. It is really a symbiosis and not a union. Now as the germ-cells are formed wholly from subepidermal and never from epidermal tissues, the seeds of these plants always produced seedlings like the type forming the *inner cell-layers.*

It seems probable that the production of the nectarine may be analogous. If the change producing the nectarine occurs after the epidermal tissue has been segregated from other tissues, the cells which are ancestors of the germ-cells should not be affected and the nectarine seedlings would give peaches. If, on the other hand, the change producing the nectarine, has occurred before any such segregation, the progeny sexually produced should in part be nectarines.